

VARIATION IN FLORAL SEXUALITY OF DICLINOUS *ARALIA* (ARALIACEAE)¹

SPENCER C. H. BARRETT²

ABSTRACT

Spatial and temporal variation in floral sexuality of diclinous plant populations influence the mating system and reproductive success of individuals. Observations of the phenology of the sex condition in andromonoecious *Aralia hispida* and dioecious *Aralia nudicaulis* indicate non-random patterns of gender expression. In *A. hispida*, cycles of male and female function resulting from developmentally synchronized protandry within ramets restrict opportunities for self- and geitonogamous pollination as well as intensify competition among staminate flowers for ovules. A ramet's male reproductive success is negatively correlated with the degree of flowering synchrony between the ramet and the population. In species with developmental synchronization of dichogamy, the evolution of large clone size will disrupt synchrony of sexual function among ramets leading to increased inbreeding. This could provide unisexual mutants with an outbreeding advantage and favor the evolution of dioecism. Genet size in *Aralia nudicaulis* is very large, precluding investigation of their frequency and distribution. In forest habitats flowering staminate ramets occur at higher densities than pistillate ramets, particularly in shaded locations. This pattern is due to differences between ramets of the sexual morphs in the frequency of flowering, possibly as a result of differential reproductive costs. Previously published data on the flowering phenology of staminate and pistillate ramets are re-interpreted in light of information showing differences in the microdistribution of flowering ramets of the sexes. Large genet size in *A. nudicaulis* can result in the spatial isolation of flowering ramets of the sexes. However, no spatial effects on the fecundity of ramets were apparent in a one hectare forest plot. The percentage fruit set in *A. nudicaulis* was substantially higher than in four co-occurring self-incompatible, entomophilous, clonal herbaceous species. This pattern of fruit set is in accord with data collected from several other plant communities and may result from the absence of functionally staminate flowers in pistillate plants of dioecious species and their importance to total fitness in hermaphrodite plants.

The mating success of individuals in diclinous plant populations is strongly influenced by spatial and temporal variation in the sexual condition of flowers. The variation is manifested at various levels including individual flowers, inflorescences, ramets, and genets during a single day, part of the flowering season, or over several years. Observations of the reproductive behavior of diclinous populations have usually revealed non-random patterns of flowering in space and time of the sexual morphs or among staminate- and pistillate-functioning flowers (Lloyd, 1973, 1974, 1981; Jong, 1976; Webb, 1976; Cruden & Hermann-Parker, 1977; Lloyd & Webb, 1977; Bawa, 1980a; Lovett-Doust, 1980; Primack & Lloyd, 1980; Bullock & Bawa, 1981; Lovett-Doust & Cavers, 1982; Lindsey, 1982; Schlessman, 1982). This has led to the formulation of a variety of hypotheses that attempt to explain the adaptive significance of variations in floral sexuality. The hypotheses involve several inter-related concepts including outbreeding advan-

tage (Charlesworth & Charlesworth, 1978, 1979; Maynard Smith, 1978; Thomson & Barrett, 1981a; Lloyd, 1982), sexual selection (Gilbert, 1975; Janzen, 1977; Willson, 1979; Bawa, 1980b; Givnish, 1980), optimal allocation of resources to maternal and paternal function (Charnov, 1979, 1982), and strategies for coping with environmental uncertainty (Thomson & Barrett, 1981b; Lloyd, 1982). Whereas the relative importance and degree of interdependence of these concepts for particular taxonomic and ecological groups are still under active debate, there is general agreement on the need for more detailed information on the factors influencing the sexual performance of individuals in natural populations.

Until recently the description and measurement of plant sexuality has lacked a quantitative basis. Inferences on the mating system of populations from observation of floral morphology alone can be particularly misleading in dichogamous species. Numerical indices of functional

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² Department of Botany, University of Toronto, Toronto, Ontario M5S 1A1, Canada.

TABLE 1. Reproductive characteristics of *Aralia hispida* and *Aralia nudicaulis* populations from central New Brunswick. From Barrett and Helenurm (1981) and Thomson and Barrett (1981).

Characteristic	<i>Aralia hispida</i>	<i>Aralia nudicaulis</i>
Major Habitat	forest clearings and open, disturbed sites	forest understory
Clone Size	small	very large
Flowering Period	July	June
Major Pollinators	bumble bees especially <i>Bombus vagans</i> and <i>B. terricola</i>	bumble bees especially <i>Bombus vagans</i> and <i>B. ternarius</i>
Breeding System	andromonoecism with synchronized protandry and self-compatibility	dioecism
Average Number Flowers per Ramet	324	♀ 75.2, ♂ 120.0
Average Flowering Time per Ramet (days)	23.2	♀ 4.9, ♂ 7.4
Fruit	fleshy fruit with 5 seeds	fleshy fruit with 5 seeds

gender (Lloyd, 1979, 1980a; Thomson & Barrett, 1981b) emphasize the quantitative and dynamic nature of sexual performance, particularly in plants with hermaphroditic flowers. Although the indices make certain unrealistic biological assumptions, e.g., panmixia, they are useful in illustrating the great variation in which individuals can succeed as pollen or seed parents and in drawing attention to the basic dichotomy in plant sexuality between populations that are monomorphic in gender and those that are dimorphic (Lloyd, 1979). These theoretical developments in combination with the use of electrophoretic techniques for estimating mating system parameters such as ovule and pollen outcrossing rates (Brown & Allard, 1970; Horovitz & Harding, 1972; Ross, 1977; Clegg, 1980; Ritland, 1983) are likely to provide new opportunities for examining the sexual performance of individuals in plant populations. They also draw attention to the fact that many aspects of plant mating are frequency dependent phenomena (Ross, 1977, 1982; Ross & Gregorius, 1983). Hence the reproductive success of an individual at a certain time will depend on the frequency, sexual condition, and fertility of the remaining individuals in the population. Studies of mating systems can be investigated accurately, therefore, only at the population level, taking into account the spatial and temporal aspects of variation in reproductive behavior.

Detailed observations of flowering patterns and

sexual performance of individuals in natural populations are available for relatively few diclinous taxa. Lloyd and Webb (1977) reviewed much of the data prior to the mid 1970s for sexually dimorphic taxa. More recent studies include Meagher (1980, 1981), Bullock and Bawa (1981), Lloyd (1981), Cox (1981, 1982), Policansky (1981), Bierzychudek (1982), Lovett-Doust and Cavers (1982). Our own studies of *Aralia* (Araliaceae) have involved an examination of flowering patterns in the sexually monomorphic *A. hispida* Vent. (Thomson & Barrett, 1981b; Thomson et al., 1982) and the sexually dimorphic *A. nudicaulis* L. (Barrett & Helenurm, 1981; Barrett & Thomson, 1982). Here I review some of these studies and make some attempt to explain the functional significance of variation in sex expression in light of various models of selection.

NATURAL HISTORY OF *ARALIA*

The four *Aralia* species of eastern North America are diclinous, perennial herbs or shrubs of wooded habitats. *Aralia nudicaulis* is dioecious, the remaining species (*A. hispida*, *A. racemosa*, and *A. spinosa*) are andromonoecious. Our work was undertaken in spruce-fir forests and associated habitats in central New Brunswick during the summers of 1978–1981. In this region *A. nudicaulis* is abundant in the understory of forests, whereas *A. hispida* is more com-

TABLE 2. Floral sexuality and fruit set (percentage of hermaphrodite flowers with mature fruit) in three andromonoecious populations of *Aralia hispida* from central New Brunswick. After Thomson and Barrett (1981).

Population (sample- size, ramets)	Total Flowers	Percentage		Fruit Set
		♀	♂	
A (N = 51)	7,407	30.0	70.0	95.8
B (N = 49)	11,893	26.6	73.4	92.2
C (N = 50)	8,926	35.0	65.0	97.2

monly encountered as a weed of disturbed sites such as forest clearings, roadsides, and burned areas. Where logging roads traverse the forest, the two species can be found growing together. Although these species share similar pollinators, their non-overlapping flowering periods preclude interspecific pollination (Table 1).

Many aspects of floral biology in *Aralia* species resemble those described for the related Umbelliferae (Müller, 1883; Ponomarev, 1960; Bell, 1971; Cruden & Hermann-Parker, 1977; Webb, 1979, 1981; Lovett-Doust, 1980; Lindsey, 1982; Schlessman, 1982). Flowers are small, whitish green, and aggregated into umbellate inflorescences. Hermaphroditic species are self-compatible and frequently exhibit complex patterns of synchronized protandry or protogyny (see below). Inflorescences of dioecious taxa occasionally contain hermaphrodite as well as staminate and pistillate flowers. However, our observations of *A. nudicaulis* in Canada and those of Bawa et al. (1982) in Massachusetts, indicate that variable sex expression of individuals is a rare condition in this species.

One of the most important ecological differences between *A. hispida* and *A. nudicaulis* is clone size. Clones (genets) of *A. hispida* are rarely larger than a few meters in diameter, with the majority being smaller. Genets are composed of one to ten ramets, most of which are reproductive. In contrast, clones of *A. nudicaulis* are very large and probably of considerable age. Field observations of isolated clones, excavation work, and mapping studies (reviewed below) suggest that in the forests studied by us genets may cover several hundred square meters, although unequivocal evidence for this is difficult to obtain. Large genets of *A. nudicaulis* are composed of hundreds of ramets, many of which are vegetative. The relative proportion of vegetative to re-

productive ramets varies with local site conditions, particularly the light regime (see below). Characters such as size, inflorescence production, and flower number per ramet in *A. nudicaulis* do not display the high degree of phenotypic plasticity exhibited by *A. hispida*.

Bumble bees are major pollinators of both *Aralia* species. Because flowers are open, small, and with anthers and stigmas borne in similar positions, any visitor is a potential pollinator. Minor visitors include andrenid and halictid bees, and syrphid flies. Foraging bees preferentially visit umbels that contain a large number of flowers, and there is some evidence that staminate-phase inflorescences are preferred over pistillate in *A. hispida* (Thomson et al., 1982). Observations of marked bumble bees indicate that individual bees restrict their foraging to a limited number of plants that they visit in regular sequences or 'traplines.' Following pollination and fertilization, fruits of both *Aralia* species develop into large, black, vertebrate dispersed, sarcochores that usually contain five seeds.

GENDER ALTERNATION IN *ARALIA HISPIDA*

Aralia hispida exhibits synchronized protandry within and among different umbels. Individual ramets pass through alternating staminate and pistillate phases during their blooming period as each umbel order flowers. Controlled pollinations demonstrate that the period of stigmatic receptivity of hermaphrodite flowers does not overlap significantly with the staminate flowering period and the probability of geitonogamy is accordingly reduced. On average a ramet functions as a male for approximately three weeks and as a female for one week. Pollen release by hermaphrodite flowers within an umbel lasts for four to five days, whereas the pistillate phase is compressed into one to two days. The overall proportion of hermaphrodite flowers in a population is approximately one-third of the total flowers (Table 2) and their numbers decline in successive umbel orders or as the season progresses. A detailed account of the floral biology and phenology of flowering of *A. hispida* is given in Thomson and Barrett (1981b).

Alternation between staminate and pistillate function in ramets of *A. hispida* results in complex patterns of gender expression within populations. A wave form pattern of floral sex ratio was evident in a population of ramets censused throughout the flowering season (Fig. 1). This

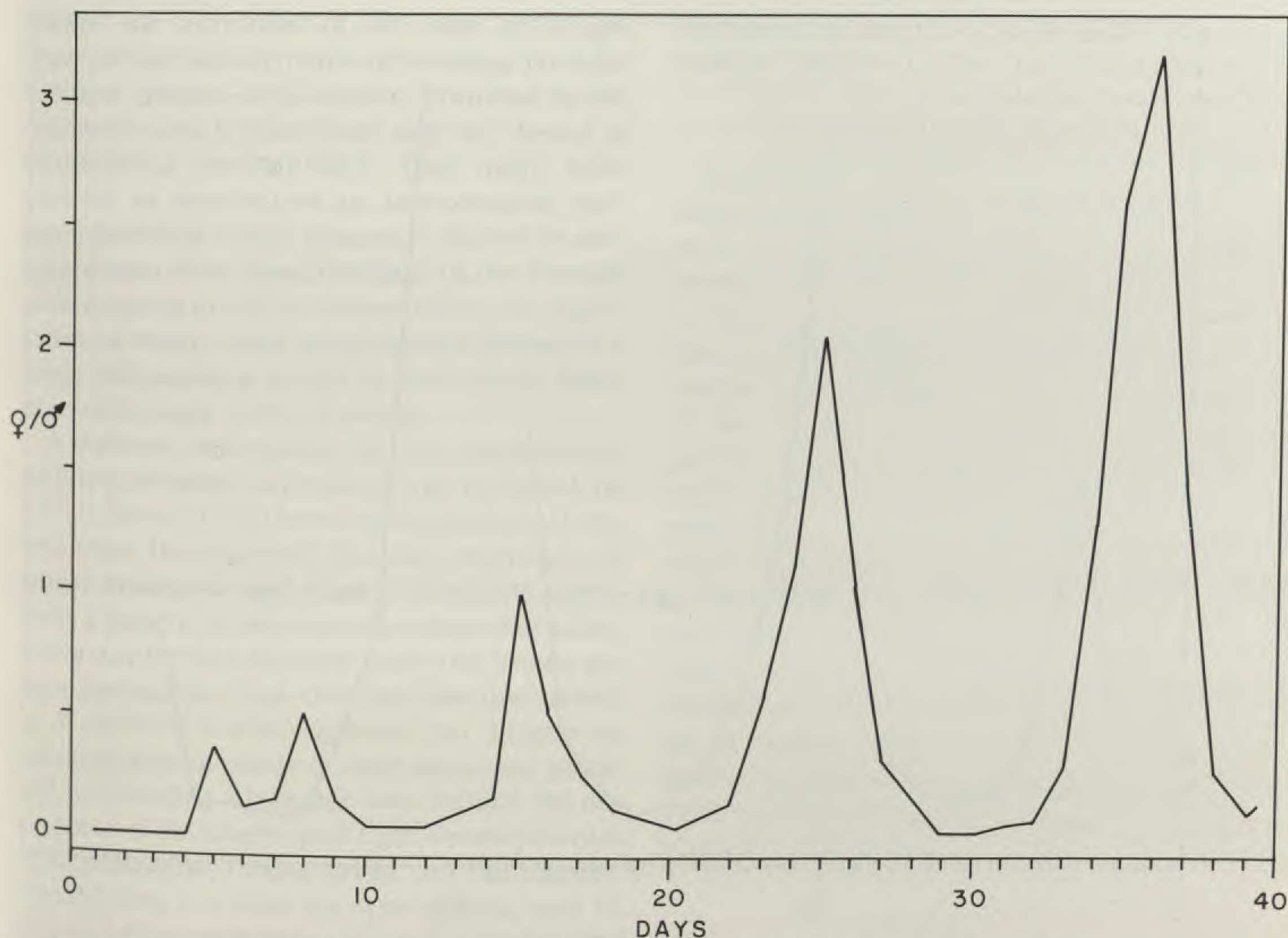


FIGURE 1. Wave form expression of gender in a population of *Aralia hispida*. The ratio of pistillate-functioning to staminate-functioning flowers is plotted daily throughout the flowering period of 48 ramets. After Thomson and Barrett (1981b).

arises, in part, from the relatively low variation among ramets in the commencement of flowering in comparison with the number of days between flowering peaks of different umbel orders. In addition, there is a marked tendency for ramets of a single genet to be developmentally synchronized with respect to umbel order and sexual condition. Intense competition for ovules among staminate-functioning flowers of different genets occurs at regular intervals during the blooming period corresponding to the troughs in Figure 1. Using estimates of functional gender one can examine the reproductive success of individual staminate- and pistillate-functioning flowers. In a population with this flowering behavior, male success is negatively correlated with the degree of synchrony between a given ramet's flowering pattern and that of the population. Ramets that produce staminate-functioning flowers at a time when most other individuals are in their pistillate phase will encounter little competition for mates. Figure 2 gives estimates of male re-

productive success for a ramet which was closely synchronized with the remainder of the population.

Selection on the male component of fitness as well as the avoidance of inbreeding may explain the complex flowering behavior in *A. hispida*. Intrasexual competition among pollen donors may account for the extended staminate phase, in comparison with the pistillate phase, of individual ramets. The gradual release of pollen over a three week period is likely to maximize the number of insect visitors and hence the potential number of mates. Within the life span of an individual flower, pollen is released gradually by sequential anther dehiscence, and nectar secretion occurs throughout the day (Thomson et al., 1982). The extended staminate phase could also have been selected to reduce the likelihood of reproductive failure owing to environmental unpredictability (Thomson & Barrett, 1981b). Unfortunately, models that invoke sexual selection or 'bet-hedging' often make qualitatively

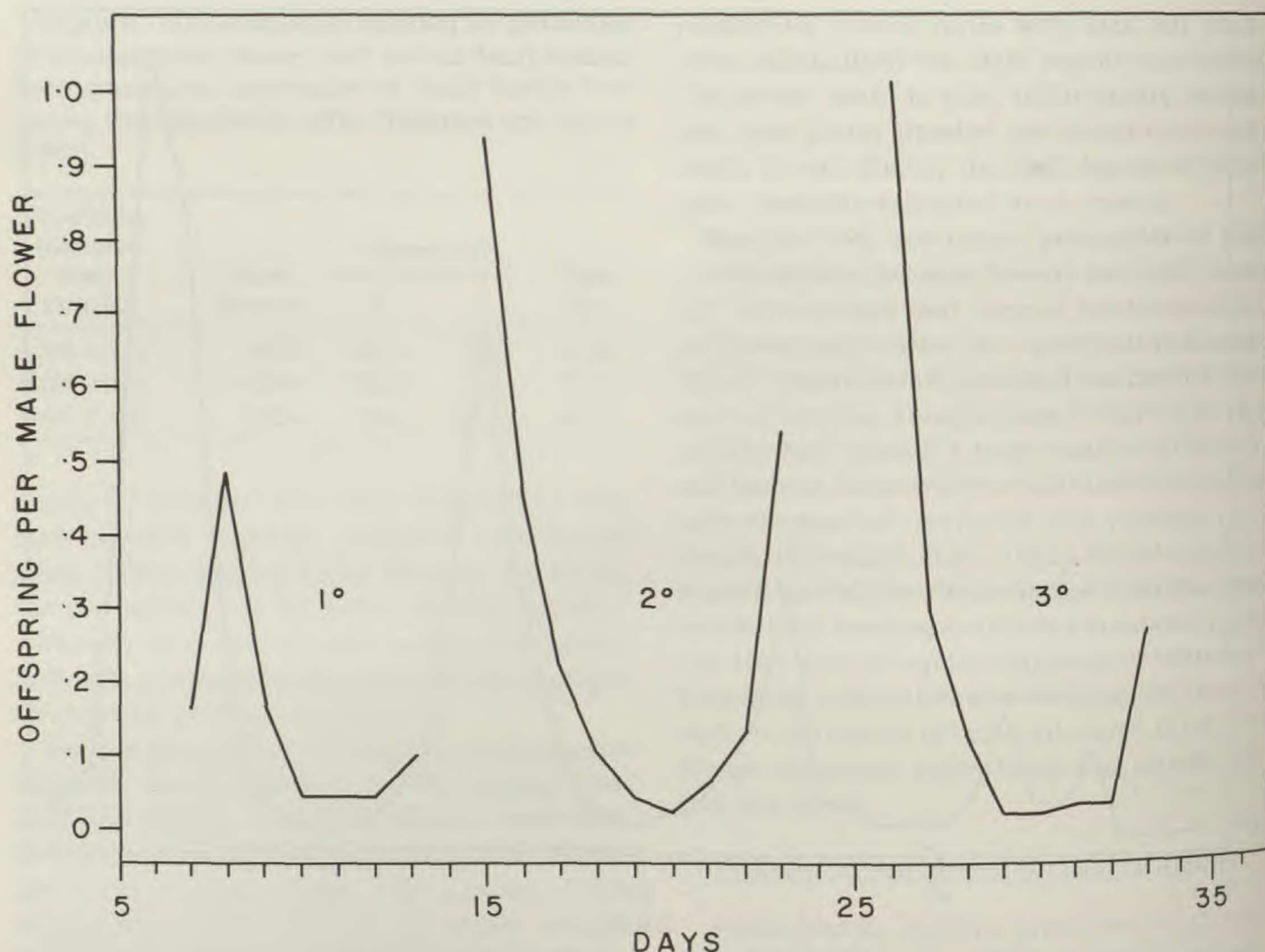


FIGURE 2. Estimate of mating success of staminate-functioning flowers of an *Aralia hispida* ramet throughout its flowering period. The flowers which are most successful are the earliest and latest within each umbel order. Breaks between the curves are days when the ramet functioned as a female. After Thomson and Barrett (1981b).

similar predictions about the evolutionary response of reproductive traits. Devising experiments to distinguish the relative importance and independence of these processes is a major challenge and reminiscent of the difficulties associated with various models of selection of self-fertilization (see Jain, 1976; Lloyd, 1980b).

Despite the protracted staminate phase of umbels, mating success via pollen tends to be concentrated at the beginning and/or end of the staminate flowering period of umbels, resulting in characteristic U- or J-shaped reproductive success curves (Fig. 2). In contrast female success is uniformly high throughout the flowering period (Table 2) and therefore there may be no selective advantage to a protracted pistillate phase. Tight flowering synchrony may be advantageous for pistillate-functioning flowers to compensate for their apparently reduced attractiveness to pollinators (Thomson et al., 1982).

Lloyd and Yates (1982) have developed ESS models to find the proportions of time that out-crossing, dichogamous, hermaphrodite flowers should spend in their staminate and pistillate phases to optimize total fitness. The models can be usefully applied to observations of flowering behavior in *A. hispida*. If paternal and maternal fitness are pollinator limited, fitness is maximized if flowers spend equal amounts of time functioning as males and females. However, where an increase in male fitness is limited by access to ovules and female fitness is limited by resources (Bateman, 1948), natural selection should favor prolongation of the staminate phase. The latter conditions fit well with the available data from *A. hispida*, in which pollinator levels are consistently high throughout the blooming period and fecundity is near maximum.

The developmental synchronization of protandry within and among umbels of *A. hispida*

reduces the likelihood of self- and geitonogamous pollination and hence inbreeding. Thus the complex systems of dichogamy exhibited by the *Araliaceae* and *Umbelliferae* may be viewed as outbreeding mechanisms. They may have evolved as alternatives to physiological self-incompatibility which appears to be rare or perhaps absent from these families. In the absence of dichogamy or self-incompatibility, the aggregation of many, small unspecialized flowers in a single inflorescence would be particularly likely to result in high levels of selfing.

A different explanation for the synchronized patterns of sexual expression was proposed by Lovett-Doust (1980) based on his studies of *Umbelliferae*. He suggested that the separation of anther dehiscence and stigma receptivity represents a pattern of resource allocation that minimizes competition between male and female gamete production. This view has been questioned by Webb (1981) who suggested that intrasexual selection among plants in their staminate phase and outbreeding advantage may explain the occurrence of protandry and tight developmental synchronization, respectively, in the family. Clearly there is a need for experimental tests to distinguish between these competing hypotheses.

The effectiveness of synchronized protandry in reducing geitonogamous pollinations depends on the degree of developmental synchronization within and between ramets of a single genet. One of the major disruptive influences to developmental synchrony among the ramets of a genet is clonal expansion. Shifts in life history associated with radiation into more stable environments could select for increased clone size. Ramets in a large clone are likely to experience widely different environmental conditions, and it seems unlikely that mechanisms could exist to maintain sexual phase synchrony with the result that geitonogamy would increase. It is possible that under these circumstances the outbreeding advantage gained by a unisexual mutant could lead to its spread, with dioecism ultimately being selected. Such an explanation could account for the associations between patterns of sexuality and plant size observed in *Aralia*. It would be of interest to examine these relationships in the *Umbelliferae* in which dioecy and various forms of dichogamy co-occur. In addition, an examination of the relative effects of self- and cross-fertilization on offspring vigor and fertility in andromonoecious taxa would be useful for

evaluating the plausibility of the outbreeding advantage model.

FLOWERING IN *ARALIA NUDICAULIS*

Populations of *Aralia hispida* are frequently composed of scattered colonies of flowering ramets, which on excavation proved to be genets. Expansion of clone size is often limited by disturbance or successional processes and hence the limits of individual genets can usually be estimated. In *A. nudicaulis* the size and complexity of the rhizome system makes identification of genets, as well as determining the sex of vegetative ramets, a difficult task. This problem is particularly acute in locally disturbed areas or where high flowering density occurs. As a result of these difficulties the unit of investigation in our studies has exclusively been the flowering ramet, composed of a single inflorescence and subtending leaf. The extent to which the behavior of ramets reflects that of the genet is unknown. In large clones it is possible that ramets separated by a considerable distance are physiologically independent (see Bawa et al., 1982).

TEMPORAL PATTERNS

The distribution of flowering ramets in *A. nudicaulis*, in time and space, was examined during the summers of 1979 and 1980. To avoid overrepresentation of individual genets, transects 1–2 km in length were adopted for sampling phenological patterns. Four transects were censused at one or two day intervals along a roadside and in forest habitats. Further details are given in Barrett and Helenurm (1981). In three of the four transects, pistillate ramets began flowering and reached peak flowering before staminate ramets. This difference was particularly evident in the two forest transects. In virtually all other studies of the flowering phenology of the sexes in dioecious species, the reverse pattern is evident (see Lloyd & Webb, 1977) and several adaptive explanations have been proposed. For example, Bawa (1980a) and Bullock and Bawa (1981) have suggested that early staminate flowering and late pistillate flowering in the small tree *Jacaratia dolichaula* (Caricaceae) may be attributed to intrasexual competition among staminate plants and mate choice by pistillate plants, respectively. Other explanations mainly associated with differential reproductive costs between the sexes are detailed in Lloyd and Webb (1977).

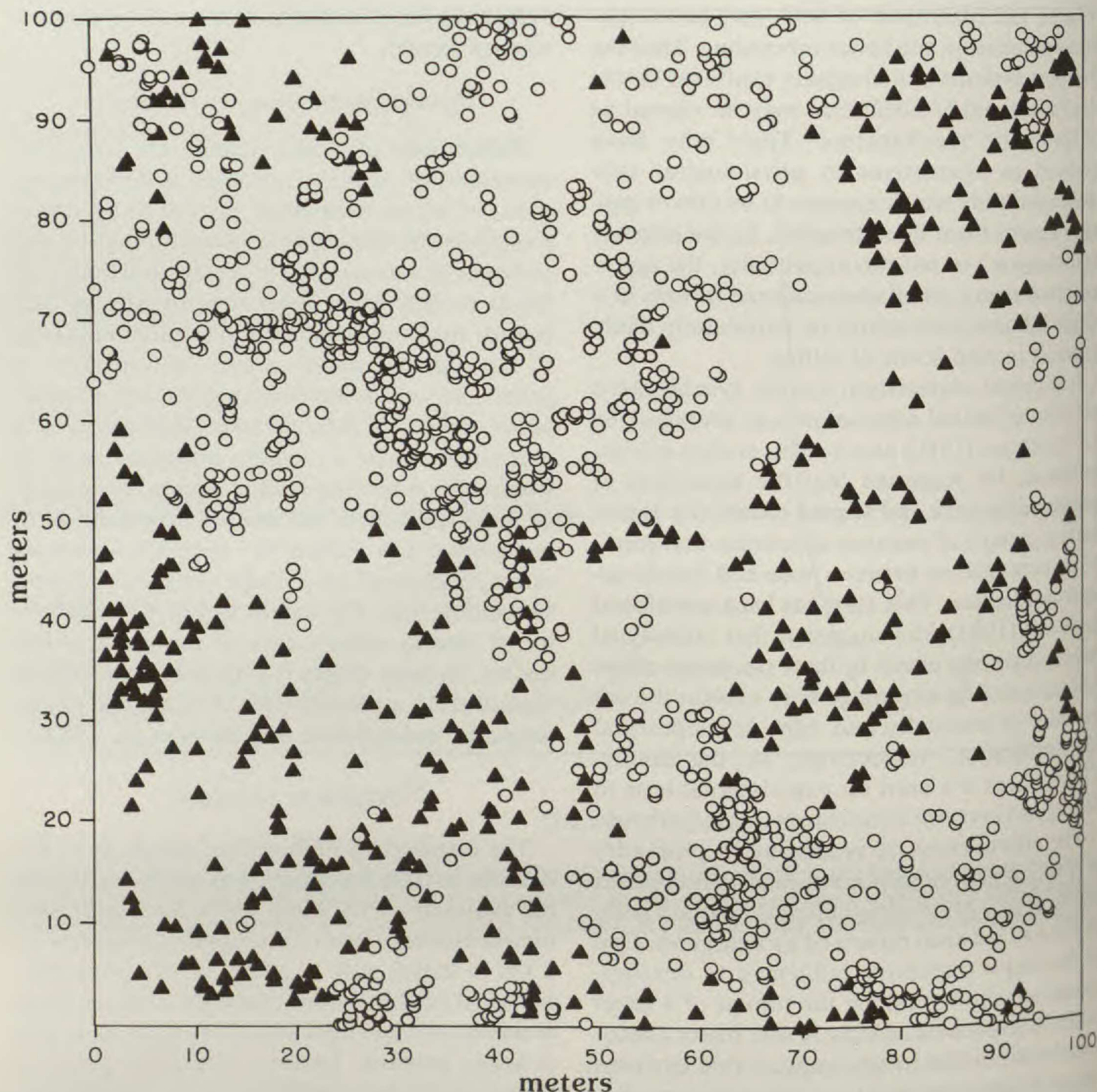


FIGURE 3. Distribution of staminate and pistillate flowering ramets of *Aralia nudicaulis* within a one hectare block of spruce-fir forest in central New Brunswick during the summer of 1979. Open circles are staminate ramets ($N = 1,244$), solid triangles are pistillate ramets ($N = 449$). After Barrett and Thomson (1982).

The flowering patterns in *A. nudicaulis* may not reflect genetic differences between the sexes in flowering time. The observed differences may result from the non-random distribution of flowering ramets of the sexes in the habitats sampled. Flowering in shaded areas tended to be delayed by several days relative to exposed sites. Examination of the spatial distribution of flowering ramets indicated that females were less likely to flower in shaded sites in comparison with males (Barrett & Thomson, 1982 and see below). In our forest transects it seems likely that the delayed flowering of staminate ramets may have

resulted from differences in the relative proportions of staminate and pistillate flowering ramets in shaded areas. It is also possible that despite our efforts to avoid over-representation of single clones in our samples through the use of long transects, genetic differences between clones in flowering time, unrelated to sex, may have been involved. These problems in the interpretation of field data on flowering behavior in *A. nudicaulis* highlight the difficulties of evolutionary interpretation of variation patterns in large clonal plants where single genets may occupy a mosaic of environments. They also draw attention

to the likelihood of interaction between spatial and temporal influences on reproductive behavior.

SPATIAL PATTERNS

The spatial relationships of flowering ramets were examined in a one hectare square block of spruce-fir forest during the summer of 1979 (for details see Barrett & Thomson, 1982). The distribution of all 1,743 flowering ramets is illustrated in Figure 3. It is tempting to suggest, based on visual inspection of the map, that several large clones of *A. nudicaulis* occupy most of the space within the forest block. A greater diversity of genetic markers than sex alone would, however, be required to distinguish individual clones. Electrophoretic studies, of the kind undertaken by Silander (1979) on *Spartina patens* would be valuable for examining the clonal structure of *A. nudicaulis* populations. Notwithstanding the difficulties of establishing the genetic aspects of population structure in the forest block, several valuable insights into the flowering behavior of *A. nudicaulis* were obtained.

By dividing the forest block into 100 10 m² by 10 m² plots, it was possible to examine associations between flowering ramets of the sexes at various spatial scales as well as with various environmental conditions. Throughout the block, as well as in other forest sites in New Brunswick (Barrett & Helenurm, 1981) and Massachusetts (Bawa et al., 1982), staminate flowering ramets outnumber pistillate. Flowering ramets of both sexes occurred more frequently in plots under an open canopy. However, there was a reduced likelihood of pistillate flowering in heavy shade in comparison with staminate ramets (Fig. 4). This may be associated with differences in the cost of reproduction in the sexes. Studies of resource allocation in *A. nudicaulis* indicate that reproductive effort in pistillate ramets is considerably higher than in androecious ramets, and that the male-biased sex ratio of flowering ramets may result from differences between the sexes in flowering propensity, particularly in forest sites (Barrett & Helenurm, 1981). Evidence to support this hypothesis was obtained by Bawa et al. (1982) from an examination of the flowering histories of staminate and pistillate ramets. Erect shoots in *A. nudicaulis* bear a series of scars left by the annual foliage leaf as well as by the inflorescence in years where flowering occurs. Hence it is possible to reconstruct the past history of flowering

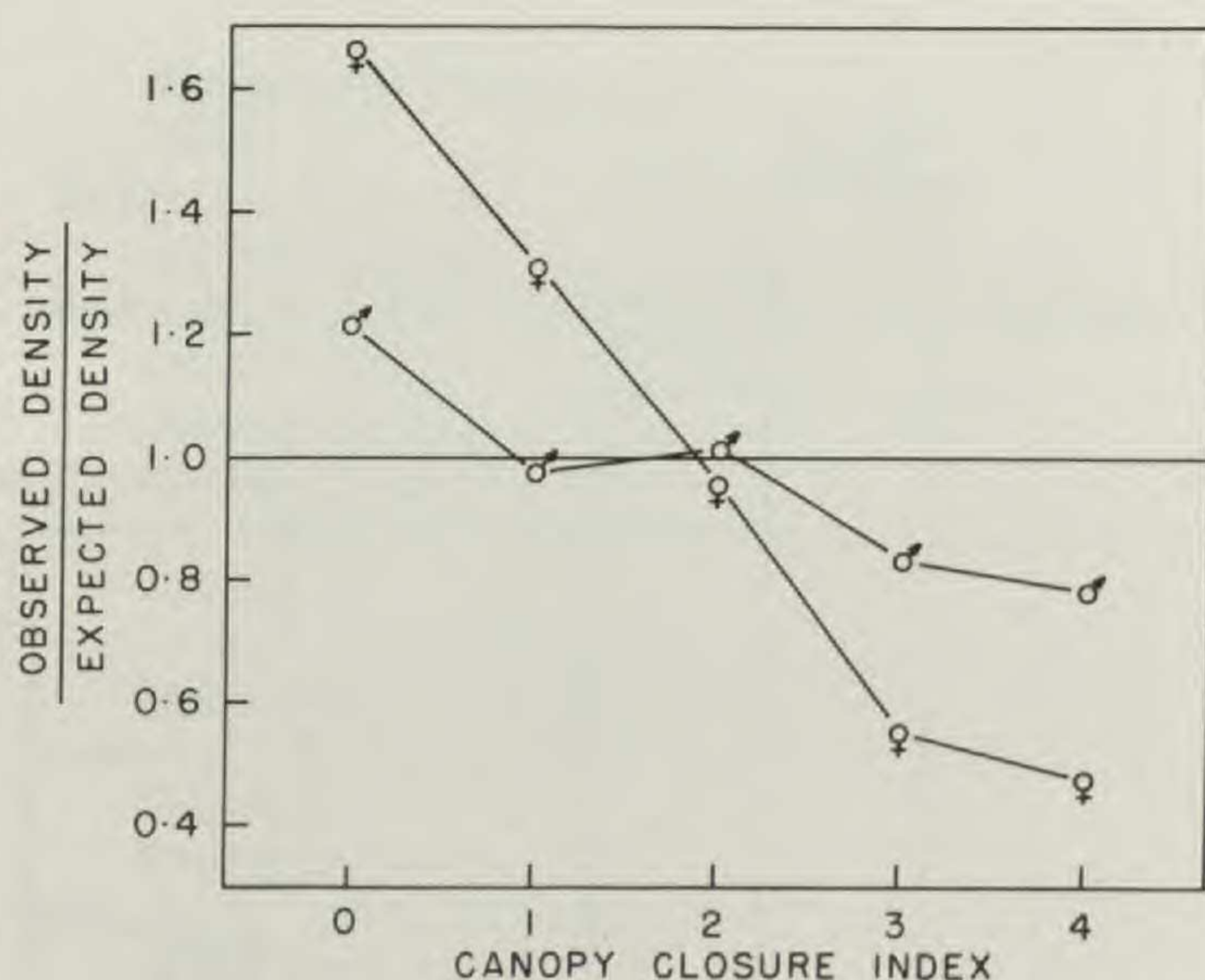


FIGURE 4. Density response of staminate and pistillate flowering ramets of *Aralia nudicaulis* to canopy closure. Closure index: 0 = most open canopy, 4 = most closed canopy. The female response is significantly stronger than the male response ($G = 18.61$, $df = 4$, $P < 0.001$). After Barrett and Thomson (1982).

of a ramet by careful dissection of individual shoots. Bawa et al. (1982) found that staminate ramets were more likely to flower in consecutive years in comparison with pistillate ramets. In addition they also found no differences between the sexes in the recruitment or mortality patterns of ramets from field observations over a three year period. Thus it seems likely that the male-biased sex ratio of flowering ramets in *A. nudicaulis* is largely the result of sex specific differences in reproductive costs.

FECUNDITY IN *ARALIA NUDICAULIS*

Inspection of Figure 3 indicates that considerable variation exists in the distance separating flowering ramets of the sexes of *A. nudicaulis*. Intersexual distance could be a potentially important influence on reproductive success. Barrett and Thomson (1982) investigated the relationships between the spatial pattern of ramets and fecundity within the forest block. Since the position of all flowering ramets in the block was known, it was possible to examine the relationships between the fruit set of pistillate ramets and the sexual composition of neighboring ramets at a range of spatial scales. No systematic variation in fecundity in relation to position was detected. At most of the biologically meaningful spatial scales, fecundity was uncorrelated with either staminate flowering density, pistillate

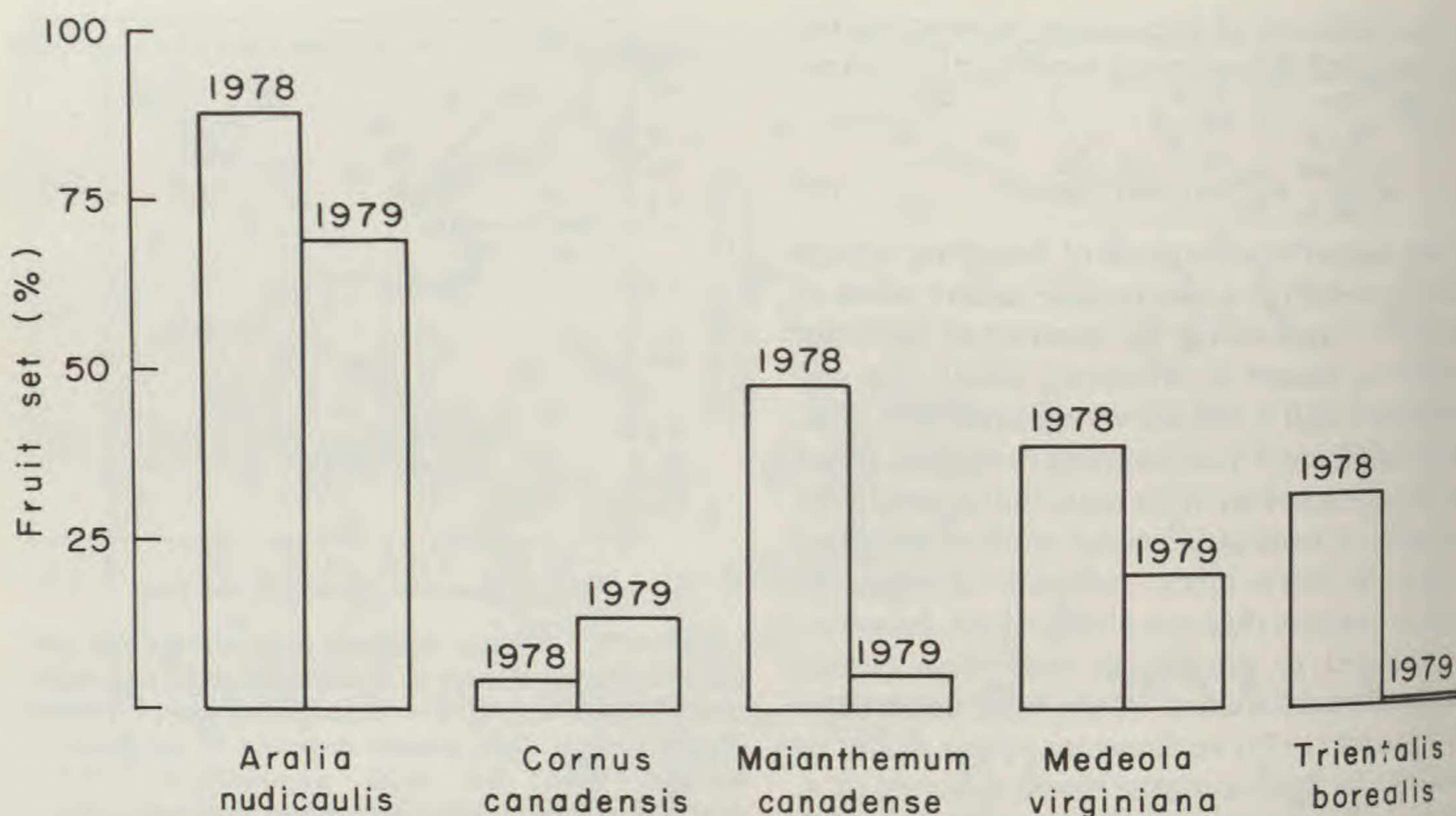


FIGURE 5. Natural levels of percentage fruit set in five entomophilous, clonal herbs from spruce-fir forests in central New Brunswick during summer 1978 and 1979. Sample sizes (flowers) for 1978 and 1979 are: *Aralia nudicaulis* 827, 20,078; *Cornus canadensis* 965, 5,069; *Maianthemum canadense* 101, 4,040; *Medeola virginiana* 63, 320; *Trientalis borealis* 69, 16. Barrett and Helenurm (unpubl. data).

flowering density or the local sex ratio of ramets. Barrett and Thomson (1982) suggested that the relatively long flight distance of bumble bees visiting the population, pollen carry over, and the predominance of staminate flowers at the site, all interact to reduce spatial effects on fecundity. Presumably at very low flowering densities isolation distances would be a more important influence on fecundity.

The fruit set of *A. nudicaulis* at the forest site averaged 68%, with the modal fecundity class 90–100%. This level was considerably higher than several other insect pollinated self-incompatible herbaceous species co-occurring with *A. nudicaulis* in this area. These species (*Cornus canadensis*, *Medeola virginiana*, *Maianthemum canadense*, and *Trientalis borealis*) share several common features with *A. nudicaulis*. All species are long-lived clonal perennials, three of the four (*C. canadensis*, *M. canadense*, and *T. borealis*) flower at the same time as *A. nudicaulis*, have relatively small white flowers and share a similar pollinator fauna (Barrett & Helenurm, unpubl. data). Of the five species only *T. borealis* does not possess fleshy fruits. The levels of fruit and seed set in *A. nudicaulis* were higher than the remaining species in the two years in which data were recorded (Fig. 5).

These results, although based on a small num-

ber of species, are in accord with predictions made by Bawa and Opler (1975) in their consideration of the pollination biology of zoophilous dioecious and self-incompatible plants. They argued that under certain conditions dioecism might be selected because it permits greater pollination success than would occur in a self-incompatible breeding system. Their arguments involve the likelihood of increased pollination efficiency in dioecious taxa as a result of the absence of 'pollen clogging' of incompatible stigmas (Shore & Barrett, 1984) as well as the increased inter-plant movement of pollinators visiting dioecious species owing to greater variation in floral rewards. Although experimental evidence to support these suggestions is limited, Bawa and Opler (1975) did report that the fruit set of dioecious species was generally higher than in self-incompatible taxa in a tropical deciduous forest in Costa Rica. A similar pattern was observed by Zapata and Kalin Arroyo (1978) in a study of breeding systems and reproductive efficacy of a secondary deciduous forest in Venezuela. More comparisons of fecundity in co-occurring dioecious and self-incompatible species are required before generalizations can be made. However, if a clear pattern emerges it may result from the fundamental differences in the nature of selection acting on inflorescences of plants with the two

breeding systems. High flower/fruit ratios in outcrossing hermaphrodites may result from selection for increased inflorescence size to enhance pollen donation and male success (Willson & Rathcke, 1974; Willson & Price, 1977). Clearly these selective forces cannot occur in seed bearing individuals of a dioecious species. Accordingly low fruit set levels in self-incompatible plants, in comparison with dioecious species, may result from the maintenance of a significant number of hermaphrodite flowers which function solely as males in self-incompatible plants (see Sutherland & Delph, 1984).

CONCLUSIONS

Our studies of the reproductive behavior of diclinous *Aralia* species document spatial and temporal variation in sexual function and enable some evaluation of the ecological consequences of sexual dimorphism. They give only limited clues, however, to the potential selective forces that maintain flowering patterns. The longevity and size of many diclinous plants restrict detailed examination of the genetic dimension so vital to evolutionary interpretations. As a result we are forced to assume that the phenotypic variation in fitness components related to sexual performance that we measure in the field has a genetic basis. Most of the literature documenting genetic effects on sexuality in higher plants involves agricultural and horticultural crops. Many examples of genes with large effects (e.g., male sterility) are reported, but there is less information on the genetics of sex expression and allocation patterns to male and female reproductive function. The available data (reviewed in Charnov, 1982) suggest that genetic variance for sex differential fertility variation within plant populations does occur (see Ross, 1982; Ross & Gregorius, 1983). However, one suspects that the high plasticity of many plant characters, particularly those involving size and flower number, as well as environmental unpredictability will complicate attempts to elucidate major fitness components. How much of the observed variance in reproductive performance in diclinous plant populations can be assigned to genetic causes is a major unresolved question.

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